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The Fossil Land Snail *Helix leidyi* Hall & Meek, 1855, a Member of a New Genus of Humboldtianidae (Gastropoda: Pulmonata)

by

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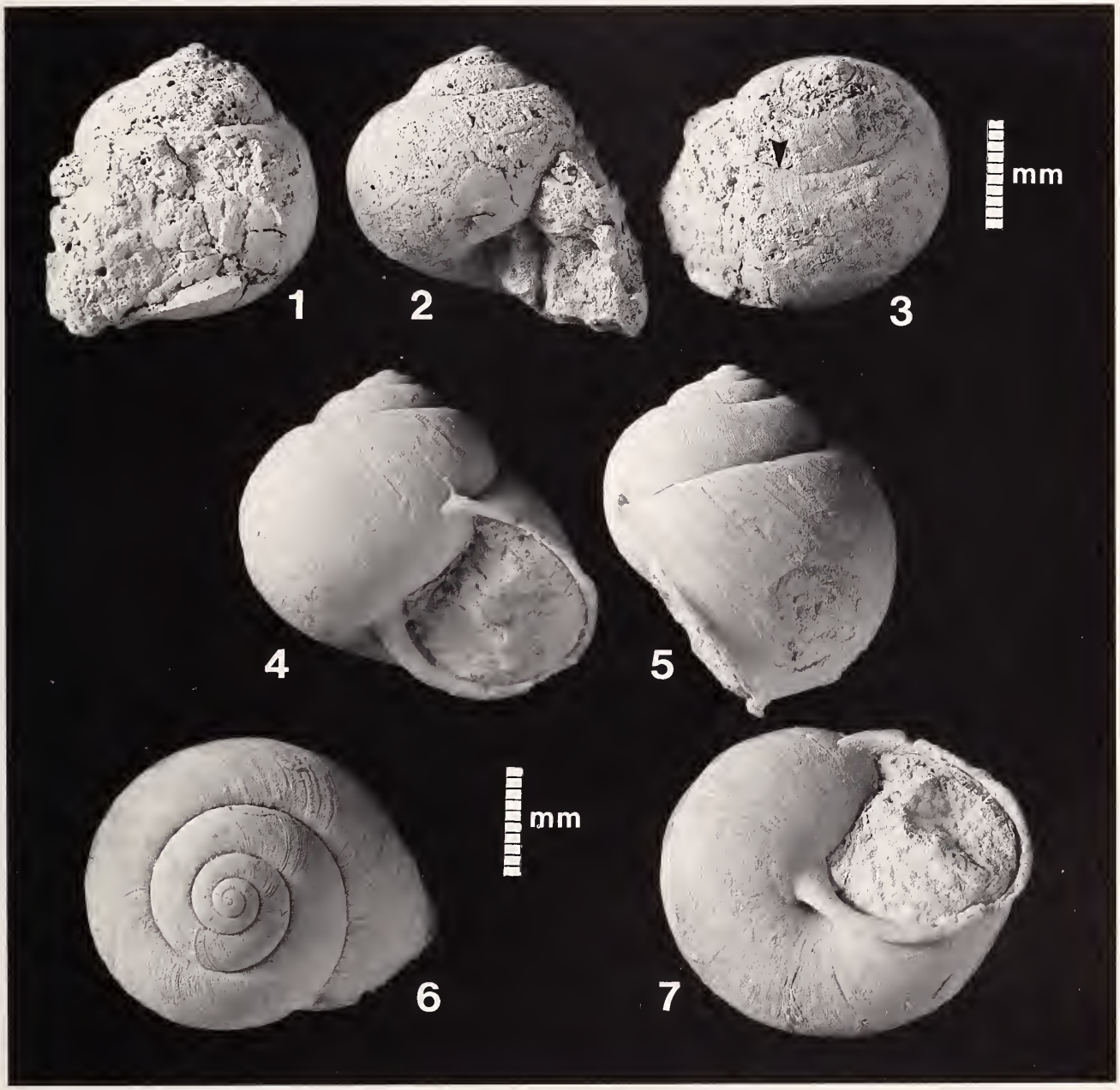
Abstract. The latest Eocene to earliest Oligocene terrestrial snail *Helix leidyi* Hall & Meek, 1855, is redescribed, based on a re-examination of the holotype and well-preserved specimens from east-central Wyoming. Much early identification of the species was based on a specimen erroneously accepted as the holotype. *Helix leidyi* is designated the type species of a new genus of Humboldtianidae, ***Skinnerelix***. ***Skinnerelix*** differs from the extant genus *Humboldtiana* von Ihering, 1892, in having a larger number of whorls, a higher spire, and a distinctly everted peristome with a slight constriction behind the basal lip. *Humboldtiana* may have originated from ***Skinnerelix*** progenetically. (Humboldtianidae, Helicidae) probably represents a Laurasian, cratonal clade with a history long independent of the Gondwanan, accretional clade consisting of (Helminthoglyptidae, Bradybaenidae, Xanthonychidae).

INTRODUCTION

Helix leidyi Hall & Meek, 1855, was the first fossil land snail species described from the western United States and has become one of the most widely cited but poorly understood species of middle Tertiary land snails. The holotype of *Helix leidyi* was collected in 1853 by F. B. Meek and F. V. Hayden in the badlands of the White River "series" in the Nebraska Territory (now western South Dakota). Subsequent to its description by HALL & MEEK (1855), classification and identification of the species were confused by the designation of an erroneous "holotype" and widespread use of the name for any large helicoid snail fossils from rocks of medial Tertiary age in the mid-continent region. Re-examination of the holotype and discovery of well-preserved specimens in east-central Wyoming (Figures 1–7) indicate that *Helix leidyi* is a member of a new genus of the Humboldtianidae. Its presence in latest Eocene and earliest Oligocene rocks of the Great Plains and central Rocky Mountains (Figure 8) has significant implications for biogeographic hypotheses concerning Humboldtianidae and Helicoidea.

The following abbreviations are used: AMNH, American Museum of Natural History, New York; UCM, University of Colorado Museum, Boulder; USNM, National Museum of Natural History, Washington, D.C.; USGS, United States Geological Survey.



Explanations of Figures 1 to 7

Figures 1–7: ***Skinnerelix*** *leidyi* (Hall & Meek, 1855).

Figures 1–3. Holotype, AMNH 11174/1, from the Scenic Member, Brule Formation, White River Group (lower Oligocene), near Scenic, Pennington County, South Dakota. Side, apertural, and oblique spire view; specimen coated for photographing; height 24.3 mm. Arrow on Figure 3 indicates point marked by arrow in Figure 9.

Figures 4–7. Figured specimen, UCM 30732, from Chadron Member, White River Formation (upper Eocene), near Douglas, Converse County, Wyoming (UCM loc. 90004). Apertural, side, spire, and basal views; specimen coated for photographing; maximum diameter 31.6 mm.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Subclass Pulmonata

Superorder Stylommatophora

Order Sigmurethra

Superfamily HELICOIDEA

Family HUMBOLDTIANIDAE

Skinnerelix Evanoff & Roth, gen. nov.

Type species: *Helix leidyi* Hall & Meek, 1855.

Generic diagnosis: Shell large (adult shells larger than 2 cm in maximum diameter); globose-conic; height to maximum diameter ratio greater than 0.8; embryonic shell smooth, consisting of first 1.2 whorls; neanic sculpture of growth rugae and coarse, somewhat crude granulation arranged in diagonal rows; last whorl broadly rounded, tumid, descending, constricted basally just behind lip; peristome flaring, narrowly turned outward, reflected at base and columella; base narrowly, obliquely perforate.

Remarks: Several features indicate assignment of ***Skinnerelix*** to the Humboldtianidae. It shares the following features with the extant genus *Humboldtiana* von Ihering, 1892: a globose-conic, narrowly perforate shell; fewer than five whorls; an embryonic shell of 1.2 whorls; coarse, rather crude granulation; and a tumid, descending last whorl. The granulation of ***Skinnerelix*** consists of close-set, round to ovate granules in diagonal rows relative to the growth lines and collabral rugae (Figures 9–11). Granulation of this type occurs in many species of *Humboldtiana,* including *H. chisosensis* Pilsbry, 1927, *H. globosa* Burch & Thompson, 1957, *H. palmeri* Clench & Rehder, 1930 (Figure 12), and *H. texana* Pilsbry, 1927. It differs from the fine, regular, fabric-like granulation found in some species of the helminthoglyptid genus *Xerarionta* Pilsbry, 1913 (*e.g., Xerarionta redimita* (Binney, 1858); see ROTH, 1984:fig. 32). In some species of *Helminthoglypta* Ancey, 1895, a still different form of granulation occurs in which close-set collabral rugae are cut into rows of elongate granules by incised spiral striae or shallow, forwardly descending sulci.

Skinnerelix differs from *Humboldtiana* in having more inflated whorls, a slightly larger number of whorls (more than 4.1 whorls compared with typically fewer than 4.1 whorls for *Humboldtiana*), a higher spire, and a distinctly everted peristome with a slight constriction just behind the basal lip. Features of adult *Humboldtiana* shells, such as the lack of an everted peristome and the small number of whorls, are characteristics of ***Skinnerelix*** shells that have not attained their full, adult growth, and suggest that *Humboldtiana* may have originated from a ***Skinnerelix***-like ancestor by a process of progenesis.

Skinnerelix occurs in upper Eocene and lower Oligocene rocks of the Big Badlands of South Dakota, the Pine Ridge of northwestern Nebraska, near Douglas, Wyoming (all, *S. leidyi*), and in the Keetley Volcanics, near Peoa, northeastern Utah (*S.* sp., *cf. S. leidyi*) (Figure 8). *Humboldtiana* is predominantly a genus of the Mexican Plateau (Figure 13), ranging from Mexico City in the south to the Guadalupe Mountains of New Mexico in the north (BURCH & THOMPSON, 1957; BEQUAERT & MILLER, 1973).

We have examined the holotype of *Humboldtiana? tuckerae* Mansfield, 1937, USNM 495934 (not 4959340, as originally published), from the Tampa Limestone, upper Oligocene of Florida. The outer lip is smoothly rolled outward a short distance, with a small internal varix that is not reflected externally in any constriction of the whorl. The inner lip is triangularly dilated over the umbilicus leaving an open, tubular, oblique perforation. Behind the aperture, the body whorl does not depart from the prior whorl trajectory and in fact descends very little.

The embryonic sculpture consists of low, obscure vermiculation overlain by widely spaced, round, flat-topped papillae. The post-embryonic sculpture consists of indistinct collabral ribs, slightly nodulose, and separated by interspaces of about the same width; small patches of short, axially elongated indentations are present. No sculpture of close-set, round to ovate granules in diagonal rows is present.

On the basis of these observations, we do not consider *Humboldtiana? tuckerae* assignable to ***Skinnerelix***. F. G. Thompson (*in* UNDERWOOD & WILSON, 1974) referred *H.? tuckerae* to the genus *Cepolis* Montfort, 1810.

UNDERWOOD & WILSON (1974) reported an unnamed species of *Humboldtiana* from the Garren Group, Hudspeth County, Texas, found in association with Chadronian Age land mammals in strata radioisotopically dated at 39–36 Ma. The specimens are crushed and distorted, with little shell surface and no adult apertures preserved. They are probably juvenile. The largest is 17+ mm in diameter, with about 3.3 whorls. Without better material, it is not possible to state whether these specimens represent *Humboldtiana,* ***Skinnerelix,*** *Xerarionta waltmilleri* Roth, 1984, as suggested by ROTH (1984), or another taxon.

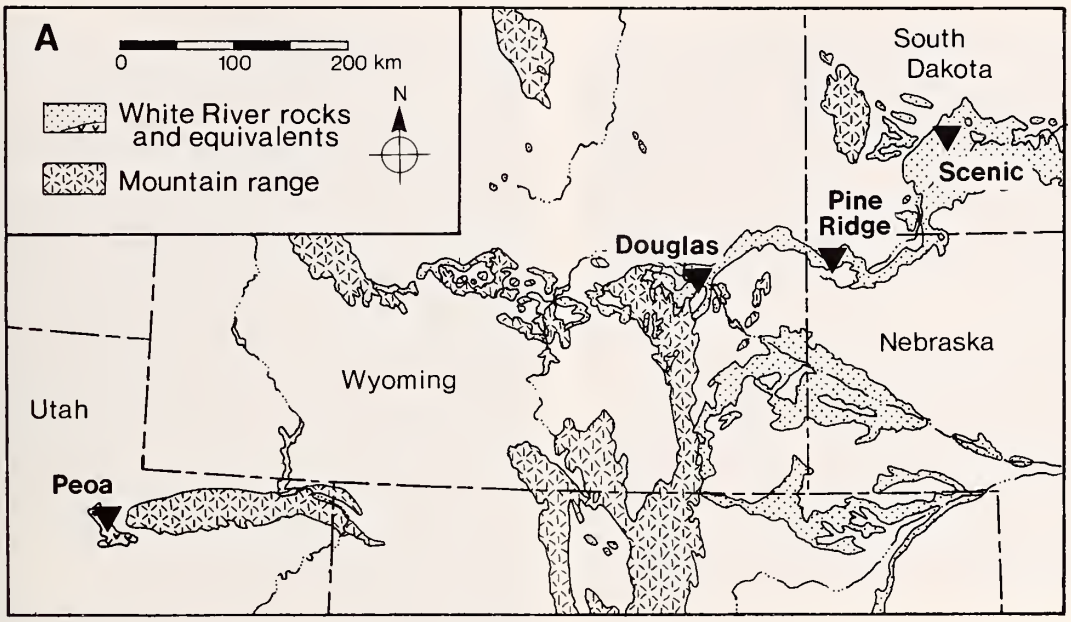
Etymology: The name ***Skinnerelix*** combines the Greek word *helix,* a spiral, hence a snail, and the name of the late Dr. Morris Skinner, collector for the American Museum of Natural History. Skinner's collections of White River land snails for the AMNH are the largest in the country, and his stratigraphic studies are the basis for many of our modern concepts of White River correlations. The gender of *Skinnerelix* is feminine.

Skinnerelix leidyi (Hall & Meek, 1855)

(Figures 1–7, 9–11)

Helix leidyi HALL & MEEK, 1855:394, pl. 3, fig. 12a, b; MEEK, 1876:604–605, pl. 45, fig. 7a, b.

?Helix leidyi Hall & Meek: WHITE, 1877:211 (in part), pl. 21, fig. 3a, b.



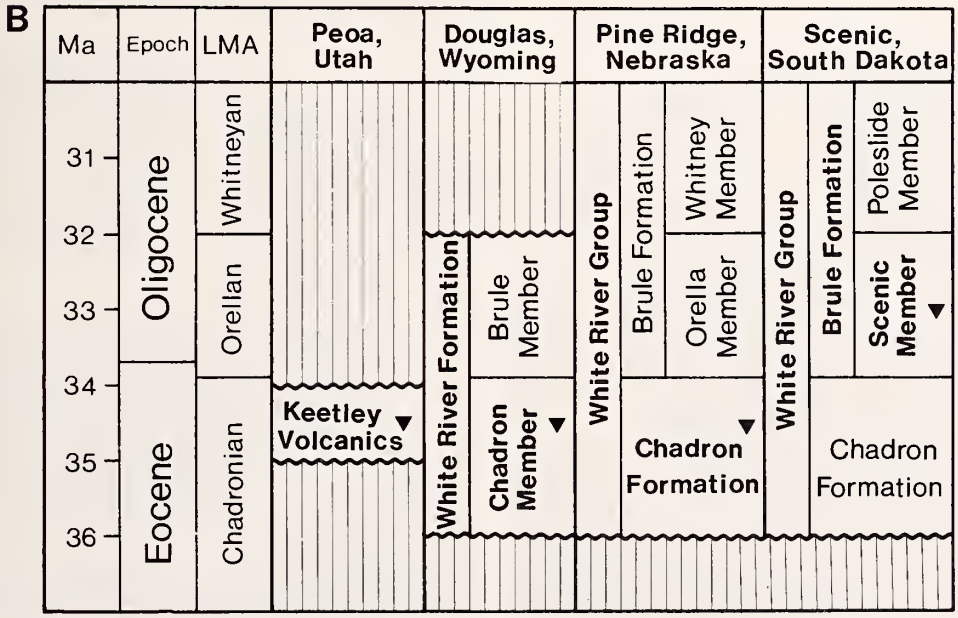
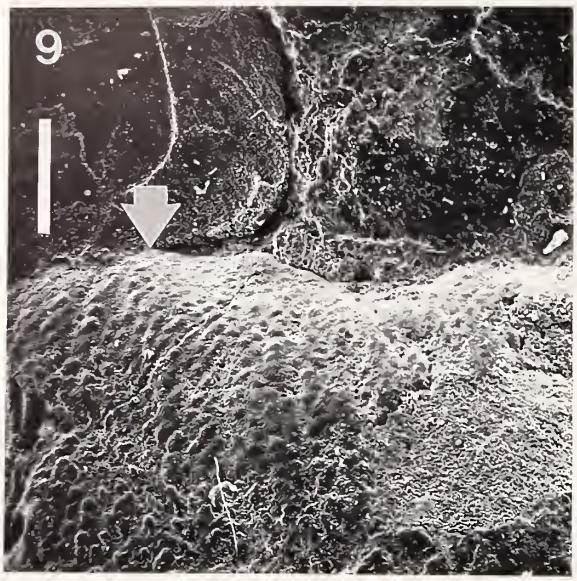


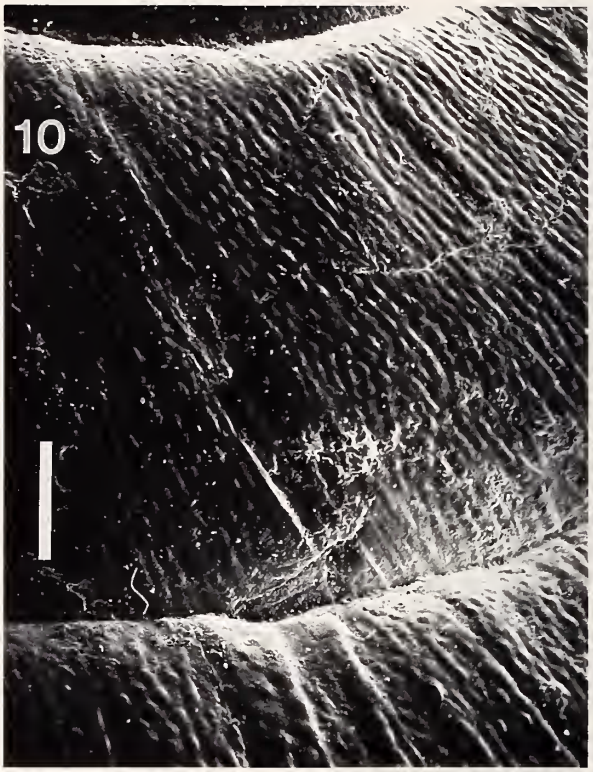
Figure 8

Distribution (A) and chronostratigraphy (B) of ***Skinnerelix*** localities.

Helix (Arianta?) leidyi Hall & Meek: White, 1883:455, 475, pl. 32, figs. 32, 33.
[*Polygyra*] *leidyi* (Hall & Meek): Hanna, 1920:9.
Polygyra leidyi (Hall & Meek): Toepelman, 1922:65.
Pseudolisinoe leidyi (Hall & Meek): Wenz, 1923:116.
Glypterpes leidyi (Hall & Meek): Zilch, 1960:655.
Non Helix leidyi Hall & Meek: White, 1877:211 (in part), pl. 21, fig. 3c; Cockerell & Henderson, 1912:232, pl. 22, figs. 1–3; Pampe, 1974:292, pl. 1, figs. 1–10.
Non Mesodon leidyi (Hall & Meek): Russell, *in* Goldich & Elms, 1949:1145.

Diagnosis: Shell large, spire broad, whorls inflated and shouldered; embryonic shell smooth, regularly increasing





Explanation of Figures 9 to 12

Figure 9. ***Skinnerelix*** *leidyi,* holotype, AMNH 11174/1. SEM photograph of diagonal granular microsculpture on apical side of last whorl, just before crushed area (see arrow on Figure 3). Bar is 1 mm long; epoxy cast of specimen coated for photographing.

Figure 10. ***Skinnerelix*** *leidyi,* figured specimen, UCM 30732. SEM photograph of diagonal granular microsculpture on last and penultimate whorls, about 0.2 whorls behind aperture. Bar is 1 mm long; epoxy cast of specimen coated for photographing.

in diameter after nucleus; sculpture of coarse granulations arranged in diagonal rows extending from adapical side to base; last whorl tumid, gradually descending in last 0.2 to 0.25 whorl.

Original description: "Shell subglobose, wider than long; spire elevated; volutions four or five, last one large and ventricose; suture distinct; surface unknown; aperture unknown; outer lip reflected; umbilicus small, or perhaps closed. The last volution .65 of whole length. The aperture is ovate, subangular behind" (HALL & MEEK, 1855:394, 411).

Description of holotype: Shell large, globose-conic, very narrowly perforate. Spire slightly convex in profile, with apical angle of 121°, sutures moderately impressed, whorls shouldered. Sculpture on penultimate and last whorls including retractive, moderately prominent growth lines and granulations arranged in diagonal rows. Last whorl tumid, rounded, descending in last 0.2 whorl; base slightly constricted upward behind lip. Peristome everted; columellar lip recurved, dilated over umbilical perforation.

Type material: Holotype: AMNH 11174/1 (James Hall number 5547/1). South Dakota, Pennington County: near the head of Bear Creek, Mauvaises Terres, turtle and bone bed (HALL & MEEK, 1855:394) collected by Meek and Hayden in 1853. About E ½, T. 3 S., R. 13 E. (HARTMAN, 1984:907); from the Scenic Member, Brule Formation, White River Group; Orellan Land Mammal Age.

Referred material (all near Douglas, Converse County, Wyoming)**:** UCM 30732 (figured), UCM locality 90004; UCM 30753, UCM locality 87063; UCM 30733, UCM locality 90004; UCM 30734, UCM locality 90005; UCM 30735, UCM locality 83235. Occurring 69.8 to 62.2 m below the top of the Chadron Member, White River Formation; Chadronian Land Mammal Age.

Additional description of referred material: The referred specimens from the Douglas area, Wyoming, are similar in size and identical in shape, sculpture of the penultimate and last whorls, and peristome morphology to the holotype, but are better preserved. The ratio of spire height to shell height in the referred specimens ranges from 0.25 to 0.31 (mean 0.27). The embryonic shells of the referred specimens consist of 1.2 smooth whorls, separated from the neanic whorls by a slight constriction, increasing whorl translation rate, and the beginning of distinct growth

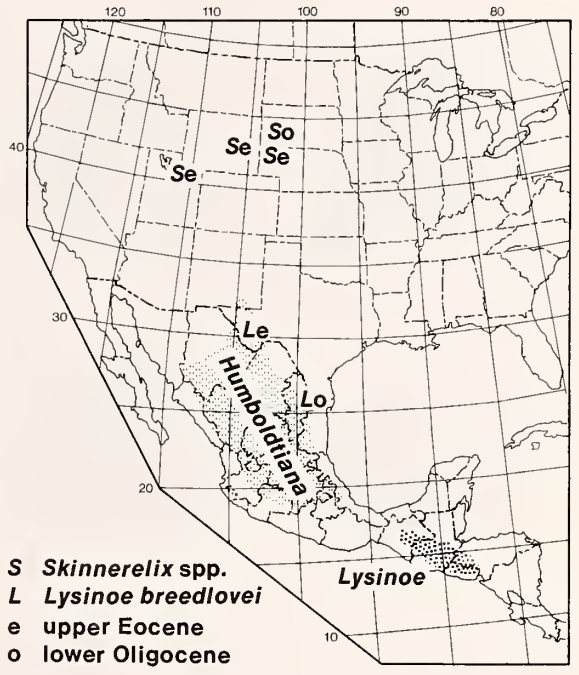


Figure 13

Distributions of modern and fossil species of ***Skinnerelix***, *Lysinoe*, and *Humboldtiana*. *Lysinoe* distribution from DALL (1897), THOMPSON (1963), ROTH (1984), and unpublished museum records. *Humboldtiana* distribution from PILSBRY (1927, 1939, 1948), SOLEM (1954, 1955), BURCH & THOMPSON (1957), and BEQUAERT & MILLER (1973).

lines. The nucleus has a typical width of 0.5 mm; the embryonic shell is not distinctly inflated after the nucleus. The neanic whorls are rounded, with granulations starting at about whorl 2, initially weak, becoming prominent after 2.75 whorls. The last whorl gradually descends in the last 0.2 to 0.25 whorl, with the lower palatal limb becoming increasingly expanded. The adapical and basal sides are slightly constricted just before the lip. Granulations are coarse and prominent on the adapical and palatal sides, weak on the base, and absent in the shallow umbilical area. The growth lines coalesce to form weak collabral rugae on the last whorl. The aperture is rounded, ovate-lunate; the outer lip is narrowly expanded on the adapical and marginal sides, recurved basally. The columellar lip is dilated and reflected. The parietal wall has a simple callus pad.

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Figure 11. ***Skinnerelix*** *leidyi*, figured specimen, UCM 30732. SEM photograph of protoconch and coarse granular microsculpture on whorls 2 and 3. Bar is 1 mm long; epoxy cast of specimen coated for photographing.

Figure 12. *Humboldtiana palmeri* Clench & Rehder, 1930, Recent, USNM 408371/1, Davis Mountains, Jeff Davis County, Texas. SEM photograph of protoconch and coarse granular microsculpture arranged in diagonal rows relative to growth lines. Bar is 1 mm long; specimen coated for photographing.

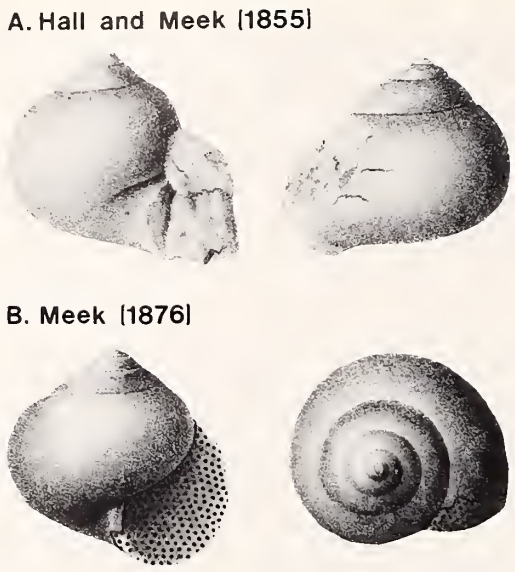

Figure 14

Original lithograph illustrations of *Helix leidyi*. A. Apertural and side views of holotype of *Helix leidyi* (AMNH 111774/1) as illustrated by HALL & MEEK (1855:pl. 3, fig. 12a, b). B. Apertural and spire views of *Helix leidyi*(?) (USNM 2102) as illustrated by MEEK (1876:pl. 45, fig. 7a, b). Specimen 26.0 mm high, maximum diameter 26.2 mm. Stippled areas represent parts of the specimen reconstructed with beeswax.

Remarks: "*Helix*" *leidyi* has been the subject of taxonomic confusion. The holotype (AMNH 111774/1) (Figures 1–3), illustrated by HALL & MEEK (1855; their illustration reproduced here as Figure 14A), is mostly an internal mold of an adult shell, with the embryonic shell and most of the spire poorly preserved. The adapical and marginal sides of the last 0.25 whorl are crushed, but shell is preserved on the adapical side of the last whorl just before the crushed area, and above this on the penultimate whorl. Despite preservational defects, the type specimen has enough features to distinguish the species from other Tertiary helicoids.

In the National Museum of Natural History is a specimen of "*Helix*" *leidyi* (USNM 2102) which is labeled "holotype," but is not the specimen illustrated by HALL & MEEK (1855). This specimen is an internal mold with no original shell and has been so over-prepared that the surface of the spire has been sculpted. The last 0.2 whorl was reconstructed with beeswax (Figure 14B). The wax reconstruction does not represent the descent of the last whorl, indicated by a slight downward reflection of the suture, and does not have a reflected lip, which is clearly preserved on the actual holotype. USNM 2102 was first illustrated by MEEK (1876) without reference to the reconstructed aperture. Unfortunately, this specimen is the one regarded by WHITE (1883), COCKERELL (1915), and subsequent workers as the type specimen of "*Helix*" *leidyi*, producing confusion in the taxonomy of the species. For example, COCKERELL (1915) could not distinguish this specimen from species of *Glypterpes* Pilsbry, 1892. On this basis, WENZ (1923) subsequently included "*H.*" *leidyi* in his genus *Pseudolisinoe,* a junior synonym of *Gypterpes.*

The specimens referred to as "*Helix leidyi*" by WHITE (1877) include one specimen (USNM 484) that may be assignable to ***Skinnerelix*** but has been greatly modified by preparation, and another (USNM 829) that is openly umbilicate and has a dome-shaped shell, features not found in *S. leidyi.*

COCKERELL & HENDERSON (1912:pl. 22, figs. 1–3) illustrated three specimens identified as "*Helix leidyi.*" One of these (AMNH 43562) has a depressed spire and a distinct umbilicus, and is not a species of ***Skinnerelix***. It is probably a member of an undescribed taxon of Whitneyan helicoids characterized by a moderately depressed spire and shouldered early whorls. The other two specimens (AMNH 43561, 43563) are poorly preserved internal molds and not identifiable.

PAMPE (1974) discussed and illustrated specimens he identified as "*Helix leidyi*" from the Eocene and Oligocene of west Texas, but ROTH (1984) reassigned them to *Lysinoe breedlovei* Roth, 1984, and *Xerarionta waltmilleri* Roth, 1984.

The systematic position of "*Helix*" *leidyi* has long been uncertain. Early workers (HALL & MEEK, 1855; MEEK, 1876; WHITE, 1883; COCKERELL, 1915) placed all large fossil helicoid-shaped snail shells from North America in the Helicidae, under the genera *Helix* Linnaeus, 1758, or *Arianta* Leach, 1831. HENDERSON (1935) and LA ROCQUE (1960) continued to refer to fossil helicoids as *Helix?* or "*Helix,*" stressing the difficulties in determining generic position from shell features alone. The family Helicidae is now considered to be native to Eurasia and North Africa. Species of *Helix* and *Arianta* have domed spires with weakly impressed sutures, tumid embryonic shells, and sculpture of spiral striations and malleations, features not found in ***Skinnerelix***.

HANNA (1920) referred "*Helix*" *leidyi* to the Polygyridae (although not explcitly to any one genus) because of its similarity to *Polygyra martini* Hanna, 1920, of the John Day Formation in Oregon. TOEPELMAN (1922), assigned ***Skinnerelix*** *leidyi* to *Polygyra* Say, 1818. Russell (*in* GOLDICH & ELMS, 1949) placed the species in the polygyrid genus *Mesodon* Rafinesque, 1821. Globose-conic polygyrids without apertural barriers, such as certain species of *Mesodon, Neohelix* von Ihering, 1892, and *Allogona* Pilsbry, 1939, have one or more of the following features: a domed spire, spiral striae, distinct radial ridges or malleations, a broadly expanded peristome, an ovate-lunate aperture, and a strong basal preapertural constriction that causes the basal wall to rise adapically. ***Skinnerelix*** *leidyi* has none of these features. Furthermore, ROTH (1987) demonstrated that *P. martini* is assignable to *Helminthoglypta,* not to the Polygyridae. *Helminthoglypta martini*

differs from ***Skinnerelix*** *leidyi* by being more widely umbilicate and having sculpture of retractive slanting riblets, spiral striae, and malleation.

COCKERELL (1915), examining figured specimens of ***Skinnerelix*** *leidyi* at the National Museum of Natural History, decided that the species was not generically distinguishable from the Eocene taxa "*Helix veterna* Meek & Hayden, 1861, "*Helix*" *riparia* White, 1876, and "*Helix*" *veterna veternior* Cockerell, 1915. Following COCKERELL (1915) in this respect, WENZ (1923) grouped these taxa into a new genus, *Pseudolisinoe,* with "*H.*" *veterna* as the type species. (*Pseudolisinoe* is an objective synonym of *Glypterpes* Pilsbry, 1892, type species "*H.*" *veterna.*) From an examination of the holotypes of *Glypterpes veterna* and *G. riparia,* we regard ***Skinnerelix*** and *Glypterpes* as distinct. Species of *Glypterpes* have more conical shells, less inflated whorls, spiral striation instead of granulation, and less everted peristomes than species of ***Skinnerelix***.

The modern species of *Humboldtiana* that most closely resembles ***Skinnerelix*** *leidyi* is *H. globosa* from the state of Vera Cruz, Mexico. Both species have highly inflated, shouldered whorls, smooth embryonic shells, and granulations arranged in diagonal rows relative to the growth rugae; both are of similar size.

Distribution and stratigraphic range: Scenic Member, Brule Formation, White River Group, Big Badlands, Pennington County, South Dakota (type locality); Orellan Land Mammal Age. Chadron Formation, White River Group, within 6 m below the top of the Chadron, Sioux County, Nebraska (USGS Cenozoic localities 20025, 22672); late Chadronian Land Mammal Age. Chadron Member, White River Formation, between 71.3 to 9.0 m below the top of the Chadron Member near Douglas, Wyoming (EVANOFF, 1990); late Chadronian Land Mammal Age. The species ranges from the latest Eocene to earliest Oligocene (late Chadronian to Orellan land mammal ages). ***Skinnerelix*** *leidyi* is common and the most obvious land snail fossil of the Chadron Member in the Douglas area. The specimens of ***Skinnerelix*** sp., *cf. S. leidyi* from the upper Eocene Keetley Volcanics (dated between 35 and 34 Ma; HINTZE, 1988) near Peoa, Summit County, Utah (USGS Cenozoic locality 23306) are too incomplete to be referred to *S. leidyi* with certainty.

BIOGEOGRAPHIC AND PALEOCLIMATIC SIGNIFICANCE

Leaving out the problematic *Humboldtiana* of UNDERWOOD & WILSON (1974), the fossil record of Humboldtianidae consists of the occurrences of ***Skinnerelix*** described above and *Lysinoe breedlovei* Roth, 1984, from the upper Eocene of Trans-Pecos Texas and the lower Oligocene of Nuevo León, Mexico. In western Texas, *L. breedlovei* ranges from the lower part of the Devils Graveyard Formation (associated with the Uintan Whistler Squat local fauna) to the Bandera Mesa Member of the Devils Graveyard Formation (associated with the early Chadronian Coffee Cup local fauna) (ROTH, 1984). All of these occurrences are older than the occurrences of ***Skinnerelix*** in the central Rocky Mountains and western Great Plains. *Lysinoe breedlovei* also occurs in lower Oligocene rocks of Nuevo León, Mexico (ROTH, 1984) that are equivalent to the Vicksburg Group (GARDNER, 1945), and about the same age as the Orellan Land Mammal Age (SWISHER & PROTHERO, 1990). By the late Eocene, at least two humboldtianid clades, that of *Lysinoe* and that of (*Humboldtiana,* ***Skinnerelix***), were differentiated.

Species of *Lysinoe* now live predominantly south of the range of *Humboldtiana* (Figure 13), and *Lysinoe breedlovei* also lived south of ***Skinnerelix***. Both clades have shifted southward since the early Oligocene, but their relative distribution has remained constant.

Humboldtiana is a plausible environmental analogue to ***Skinnerelix***. *Humboldtiana* ranges from Mexico City, Mexico, north to the Guadalupe Mountains in southeast New Mexico (Figure 13). It typically lives in a variety of substrates and woody vegetation, ranging from oak forests on limestone to high coniferous forests and mixed scattered woodlands on volcanic rocks (PILSBRY, 1939).

The climate in the range of *Humboldtiana* is subtropical, as defined by WOLFE (1979), with mean annual temperatures ranging from 13 to 21°C, and mean annual range of temperatures of 4–20°C (WERNSTEDT, 1972; WORLD METEOROLOGICAL ORGANIZATION, 1979). The presence of a land snail with subtropical affinities in the Rocky Mountains during the late Eocene is consistent with paleoclimatic interpretations based on the contemporaneous Florissant flora of Colorado (MACGINITIE, 1953).

The classification of the Helicoidea is in a state of flux (along with the rest of the Stylommatophora; see EMBERTON *et al.,* 1990), with opinions varying as to the relationships of the Humboldtianidae (*e.g.,* SCHILEYKO, 1978, 1979, 1991; NORDSIECK, 1987; TILLIER, 1989). A robust phylogenetic hypothesis is only now coming into place for the families of Helicoidea. (The wide-ranging paper of SCHILEYKO [1991] was published almost simultaneously with submission of the present paper; Roth [in preparation] has some rather different ideas about the genera of Helminthoglyptidae.) We regard the Humboldtianidae as a holophyletic group (*sensu* ASHLOCK, 1971), defined by the synapomorphies of a ring of nodular mucus glands surrounding the vagina at a single level, subtended by a ring of dart sacs sessile on the vagina.

In the view of SCHILEYKO (1978, 1991; personal communication to Roth, 1990) the condition of multiple mucus glands seated around the vagina and multiple sessile dart sacs is primitive relative to the smaller number of dart sacs (generally one) and more closely adjacent mucus glands found in Helicidae and in secondarily simplified genera such as *Leptarionta* Fischer & Crosse, 1872. It is morphologically closer to the hypothesized ancestral condition

in which the vaginal wall is extensively glandular and furnished with aragonitic spicules. The branching diagram of SCHILEYKO (1978:fig. 29) contains the clade ((Humboldtianidae, Helicidae), (Bradybaenidae, Helminthoglyptidae)); but the apomorphies (if any) defining the branch segments are not specified.

The cladogram of NORDSIECK (1987:fig. 30) includes Humboldtianidae within a heterogeneous family Xanthonychidae, separated from (Bradybaenidae, (Hygromiidae, Helicidae)) by the single, equivocal character of "dart glands [= mucus glands] not divided/divided." But in the bradybaenid genus *Aegista* Albers, 1850, for example, the mucus glands range from single to multiple, with variously one, two, or perhaps more insertions on the nebensack (AZUMA, 1982). In the helminthoglyptid genus *Micrarionta* Ancey, 1880, the glands are paired; in *Helminthoglypta* they could be said to be divided—there are two bulbous reservoirs leading into the common duct—even though they ultimately form a single membranous envelope around the dart apparatus.

MILLER & NARANJO-GARCÍA (1991) pointed out the correspondence between the distribution of the helicoid families Bradybaenidae, Helminthoglyptidae, and Xanthonychidae and the tectonically accreted terranes around the Pacific Rim. From this pattern they drew the conclusion that those families had a common ancestry on a Mesozoic Gondwanan land mass ("Pacifica"; see NUR & BEN-AVRAHAM, 1977; JONES *et al.*, 1982) and were dispersed passively to Asia and the Americas on rafting fragments of continental crust. They also noted that the distribution of Humboldtianidae does not correspond to any accretional realm, and therefore excluded the family from the above scenario. Humboldtianidae must have had a history independent from that of the "Pacifican" families. Recognition of ***Skinnerelix*** as a genus of Humboldtianidae does not alter, and in fact reinforces, the model in this respect.

(Stratigraphic evidence is not well in accord with the "Pacifica" hypothesis for the origin of Helminthoglyptidae. The earliest fossil occurrences of *Helminthoglypta* (*H. bozemanensis* Roth, 1986), *Xerarionta* (*X. waltmilleri*), and *Polymita* (*P. texana* Roth, 1984) are an old continent, not accreted terrane. However, a thorough review of the fossil evidence, taking into account the uneven distribution of fossiliferous terrestrial deposits of critical ages, has yet to be made.)

Combining the phylogenetic hypothesis of SCHILEYKO (1978, 1991) and the historical zoogeography of MILLER & NARANJO-GARCÍA (1991) produces the following model: (Humboldtianidae, Helicidae) represents one (Laurasian, cratonal?) clade, with vicariance between the two families possibly related to the development of the Atlantic Ocean as a dispersal barrier. (Helminthoglyptidae, Bradybaenidae, Xanthonychidae) represents a second (Gondwanan, accretional?) clade, with possible vicariance related to the breakup of "Pacifica." Sympatry between members of these two clades (*e.g.*, Recent *Sonorella* and *Humboldtiana* in northern Mexico, on old continent) must therefore be the result of dispersal (in this example, presumably of the helminthoglyptid into humboldtianid territory). Dispersal of the Gondwanan clade in North America must have proceeded from accreted to cratonal terrane.

Analysis of further characters of the snails themselves can (and should) be used to test the phylogenetic component of this model. The stratigraphic and geographic distribution of the respective clades can be used to test, and develop a time scale for, the historical component. This model predicts that, in paleoenvironments that could support snails of both clades, the home clade will appear stratigraphically below the first appearance of the dispersing clade.

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Appendix

Locality register of figured and referred specimens.

UCM locality number	Location	USGS 7½ min. quadrangle map
83235	260 m W, 260 m N of SW corner, sec. 28, T. 31 N, R. 70 W	Dilts Ranch, WY (1949)
87063	380 m E, 1070 m S of NW corner, sec. 27, T. 31 N, R. 70 W	Orin, WY (1949)
90004	60 m W, 500 m N of SE corner, sec. 28, T. 31 N, R. 70 W	Cedar Hill, WY (1949)
90005	280 m W, 1300 m S of NE corner, sec. 29, T. 31 N, R. 70 W	Irvine, WY (1949)